TERTIARY HOLASTEROID ECHINOIDS FROM AUSTRALIA AND NEW ZEALAND

by R. J. FOSTER *and* G. M. PHILIP

ABSTRACT. All known holasteroid echinoid species from the Tertiary rocks of Australia and New Zealand are described and illustrated. All except *Echinocorys australis* sp. nov., from the Palaeocene of Western Australia, belong to genera confined to Australia and New Zealand. Other holasterids are *Giraliaster jubileensis* gen. et sp. nov. with additional species *G. tertiarius* (Gregory), *G. sulcatus* (Hutton) (= *Cardiaster latecordatus* Tate), and *G. bellissae* sp. nov. A new family Corystidae is proposed for holasteroids with a central rostral plate. Included in the family are *Corystus dysasteroides* (Duncan) (= *Duncaniaster australiae* (Duncan) = *Galeraster australiae* Cotteau), *Cardabia bullarensis* gen. et sp. nov., and *Huttonechinus spatangiformis* (Hutton) gen. nov. The distribution of holasteroid echinoids in Australia and New Zealand indicates shallow water connection between the Southern Ocean and the Tasman Sea from the Palaeocene onwards, and that west–east trans-Tasman migration of echinoids has proceeded throughout the Cainozoic. The holasteroids provide evidence against the concept of a relatively cosmopolitan echinoid fauna in southern Australasia during the Palaeocene to Miocene. The precursors of the fauna, prior to the separation of Australia from Antarctica, are to be sought in the Indian Ocean area.

HOLASTEROID echinoids comprise a numerically small, yet diverse and significant component of the abundant Tertiary echinoid faunas of Australia and New Zealand. For this article we have examined all known material, a task which has taken several years since the material is scattered through many repositories and museums.

The occurrence of holasteroid echinoids in the Australian Tertiary was well known in the last century through the work of Duncan (1877, 1887), Gregory (1890), and Tate (1892). The group constitutes the main evidence for a still prevailing view on the palaeogeographic relationship of the fauna. Gregory (1890, p. 491) succinctly described the fauna thus, 'It seems to be composed of two constituents: about one third of the species are of ordinary Palaearctic Upper Cretaceous genera; these seem to have migrated southwards and become mingled on their journey with a fauna that agrees more closely with that of the Eocenes of India and Malaysia'. Fell (1953) has echoed this interpretation and more recently (1971) has even maintained that undisclosed echinoids serve to indicate that peninsular India has occupied its present position since at least the late Jurassic. Even Henderson (1975), viewing the New Zealand Tertiary spatangoids, concluded that (p. 7) 'Palaeocene–Miocene faunas of the world are dominated by cosmopolitan and widely distributed genera which appear to have been distributed largely from centres in the tropical Atlantic and Mediterranean regions into the Indo-Pacific'.

In this revision, holasteroids previously placed in genera such as *Holaster* and *Cardiaster* are referred to five genera, three of them new, and four known only from late Cretaceous and Tertiary strata of Australia and New Zealand. A new family is proposed to accommodate three Australian and New Zealand genera which are set well apart from other holasteroids in the nature of the plastronal plating. Of the eight species described here, only one, *Echinocorys australis* sp. nov., is referred to a cosmopolitan holasteroid genus. Holasteroid echinoids therefore support the view of

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a strongly endemic nature for the Australasian Palaeogene fauna (cf. Philip and Foster 1971).

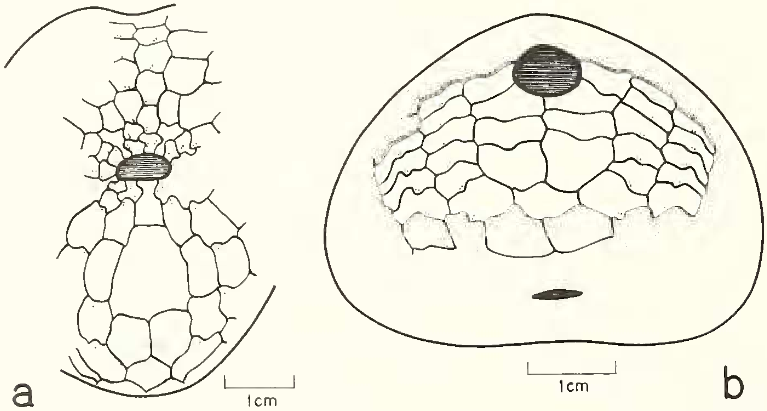
The Australasian Tertiary holasteroid fauna, although largely endemic at the generic level, is of more than local interest. It provides an example of continued diversification and evolution in the Cainozoic of a group that declined abruptly at the end of the Cretaceous in the northern hemisphere. Such diversification is typical of the Palaeogene echinoid fauna of southern Australia as a whole and is presumably the result of new ecological opportunities brought about by the rifting of Australia from Antarctica and the opening of the Southern Ocean. The fauna also provides evidence of completion of this seaway between Antarctica and Australia at a time earlier than has hitherto been recognized.

The following abbreviations are used to designate the various repositories: AUGD—Adelaide University Geology Department, Adelaide, S.A.; BM—British Museum (Natural History), London; CPC—Commonwealth Palaeontological Collection, BMR, Canberra; NMV—National Museum of Victoria, Melbourne, Victoria; NZGS—New Zealand Geological Survey Museum, Lower Hutt, N.Z.; OU—Otago University Geology Department, Dunedin, N.Z.; SAM—South Australian Museum, Adelaide, S.A.; WAM—Western Australian Museum, Perth, W.A. Undesignated material is in the R. J. Foster Collection.

SYSTEMATIC PALAEONTOLOGY

Order HOLASTEROIDA Durham and Melville, 1957
Family CORYSTIDAE fam. nov.

Diagnosis. Rounded holasteroids, with anterior notch either feeble or absent and with a subanal rostrum; ambulacra non-petaloid. Apical system disjunct with three or four genital pores. Plastron modified meridosternous with the first pair of episternal plates followed by a single central rostral plate. Subanal fasciole present, encircling the rostral plate.



TEXT-FIG. 1. *Corystus dysasteroides* (Duncan). *a*, plating of adoral surface showing rostral plate, based on SAM P18011 from Tailem Bend, South Australia. Position of subanal fasciole inferred from other specimens. *b*, posterio-oral view of pre-anal, rostral, and episternal plates of the posterior interambulacrum, based on NMV P31229 from Waurn Ponds, Victoria.

Included genera. Corystus Pomel, 1883; *Cardabia* gen. nov.; *Huttonechinus* gen. nov.

Remarks. The presence of the post-episternal rostral plate sets this family well apart from other holasteroids and must be regarded as a specialized development. As lateral fusion of plates cannot be invoked to explain its origin (cf. Mortensen 1950, p. 37) the plastron of the Corystidae must be viewed as a modification of an advanced meridosternous (metasternal) condition. The rostral plate sees no parallel in other echinoids.

The new family is known only from Tertiary strata of Australia and New Zealand, although a similar-looking but poorly known genus, *Basseaster* Lambert from the Maastrichtian of Madagascar, may prove to belong to the family. The family first appeared in the Palaeocene of north-western Australia, and was present at a number of localities along the south coast of Australia by the late Eocene. It reached New Zealand in the Oligocene, and died out in both countries during the early Miocene. Its total range is probably P4 to N8 in the letter zonation of Berggren (1969).

Genus CORYSTUS Pomel, 1883

1883 *Corystus* Pomel, pp. 61–62.
1890 *Galeraster* Cotteau, p. 548.
1896 *Duncaniaster* Lambert, p. 317.
1903 *Duncaniaster* Lambert; Lambert, p. 32.
1921 *Galeraster* Cotteau; Lambert and Thiéry, p. 332.
1924 *Cibaster* (*Duncaniaster*) Lambert; Lambert and Thiéry, p. 408.
1946 *Duncaniaster* Lambert; Clark, p. 361.
1948 *Galeraster* Cotteau; Mortensen, p. 84.
1950 *Duncaniaster* Lambert; Mortensen, p. 74.
1953 *Duncaniaster* Lambert; Fell, pp. 246–249.
1966 *Galeraster* Cotteau; Wagner and Durham, p. U445.
1966 *Duncaniaster* Lambert; Wagner and Durham, p. U528.
1968 *Duncaniaster* Lambert; Eames, p. 367.
1971 *Duncaniaster* Lambert; Davies, p. 142.
1976*a* *Corystus* Pomel; Foster and Philip, pp. 113–116.

Type species. Rhynchopygus dysasteroides Duncan, 1877; by monotypy. The type species of *Galeraster* is *G. australiae* Cotteau, 1890, and of *Duncaniaster* is *Holaster australiae* Duncan, 1877.

Diagnosis. Moderate sized, domed holasteroids with a faint frontal notch and low plastronal keel. Disjunct apical system with four genital pores located in front of centre. Ambulacra all similar, flush with test and subpetaloid, with small circular pores placed close together; pores paired throughout. Periproct transversely oval, situated above anal rostrum at termination of the posterior slope of the test. Peristome in front of centre, with prominent phyllodes; paired interambulacra amphiplacous. Labrum comparatively broad and not protruding. Subanal fasciole subcircular, enclosing the rostral plate.

Remarks. The complex nomenclatorial history of the type species of this genus has been discussed by Foster and Philip (1976*a*), who concluded that it is conspecific with both *H. australiae* Duncan (type species of *Duncaniaster* Lambert), and *Galeraster australiae* Cotteau (type species of *Galeraster* Cotteau). At present only the one species of *Corystus* is recognized, although *C. dysasteroides* is acknowledged to show considerable variation in time (Foster and Philip 1976*b*). The distribution of the species is discussed below.

Lambert's genus *Basseaster* (1936, p. 23) closely resembles *Corystus* in its inconspicuous ambulacral pores, very slight frontal notch, keeled plastron, anal rostrum surrounded by a fasciole, and the character of its tuberculation. Lambert described the apical system as comprising one elongate plate without sutures; however, there are four genital pores, with the posterior pair well separated from the anterior pair. Lambert could not discern the vital sutures of the plastron. The only known species is *B. rostratus* (Lambert 1936, pp. 23, 24, pl. 3, figs. 8–12; pl. 4, fig. 10) from the Maastrichtian of Madagascar.

Corystus dysasteroides (Duncan, 1877)

Plate 85, figs. 1–5; Plate 86, figs. 1–5; text-fig. 1

1877 *Rhynchopygus dysasteroides* Duncan, p. 49, pl. 3, figs. 9, 10.
1877 *Holaster australiae* Duncan, p. 51, pl. 3, figs. 12, 13.
1883 *Corystus dysasteroides* (Duncan); Pomel, p. 61.
1887 *Holaster australiae* Duncan; Duncan, p. 420.
1887 *Holaster difficilis* Duncan; Duncan, p. 421.
1890 *Galeraster australiae* Cotteau, p. 548, pl. 12, figs. 16–18.
1890 *Holaster difficilis* Duncan; Gregory, p. 490.
1891 *Holaster australiae* Duncan; Tate, p. 276.
1892 *Holaster australiae* Duncan; Bittner, p. 359, pl. 3, fig. 3.
1892 *Holaster australiae* Duncan; Tate, p. 193.
1893 *Lampadocorys australiae* (Duncan); Lambert, p. 97.
1896 *Duncaniaster australiae* (Duncan); Lambert, p. 317.
1921 *Galeraster australiae* Cotteau; Lambert and Thiéry, p. 332.
1921 *Rhynchopygus dysasteroides* Duncan; Lambert and Thiéry, p. 364.
1924 *Cibaster* (*Duncaniaster*) *australiae* Duncan; Lambert and Thiéry, p. 408.
1946 *Duncaniaster australiae* (Duncan); Clark, p. 361.
1948 *Galeraster australiae* Cotteau; Mortensen, p. 84, fig. 62.
1950 *Duncaniaster australiae* (Duncan); Mortensen, p. 74, fig. 66.
1970 *Corystus dysasteroides* (Duncan); Foster *in* Lindsay, p. 9.
1970 '*Duncaniaster*' *australiae* (Duncan); Philip, p. 184, figs. 5A, D.
1971 *Duncaniaster australiae* (Duncan); Davies, figs. 349A, B.
1976*a* *Corystus dysasteroides* (Duncan); Foster and Philip, p. 113, figs. 1, 2.
1976*b* *Corystus dysasteroides* (Duncan); Foster and Philip, p. 129, figs. 1–3.

Material and occurrence. Several hundred specimens are available (R. J. Foster Collection) from a considerable number of localities in Victoria, South Australia, and Western Australia, and Foster and Philip (1976*b*) provide details of this material. The holotype, BM E42418, is from the Castle Cove Limestone, Castle

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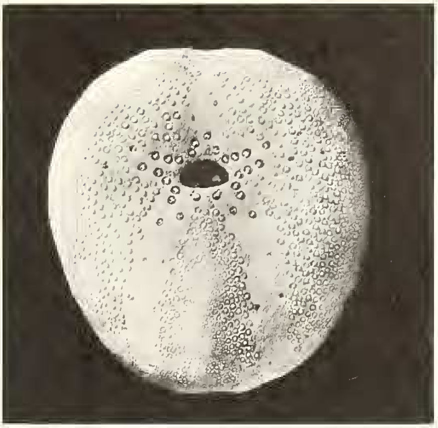
EXPLANATION OF PLATE 85

Figs. 1–5. *Corystus dysasteroides* (Duncan). 1, adoral view of SAM P18012, Wool Bay, Yorke Peninsula, South Australia, ×1. 2, adapical view of NZGS EC824, Gees Point, Gee Greensand, New Zealand, ×1. 3, enlargement of apical system of NMV P18552, Waurn Ponds, Victoria, ×5. 4, adapical view of SAM P18013, a specimen with flexed posterior ambulacra petals, Wool Bay, Yorke Peninsula, South Australia, ×1. 5, posterior adoral view of a weathered specimen showing the sutures between the sternum, the episternals, and the central rostral plate, SAM P18016, Wool Bay, Yorke Peninsula, South Australia, ×2.



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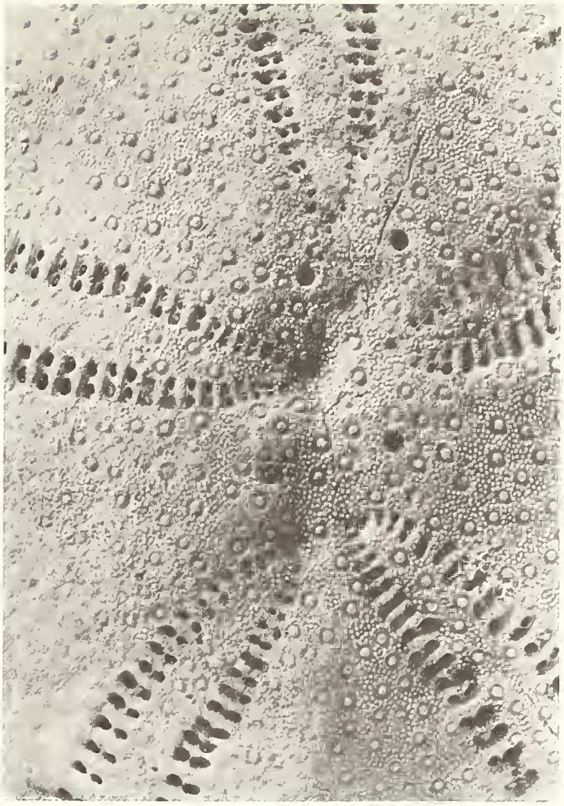

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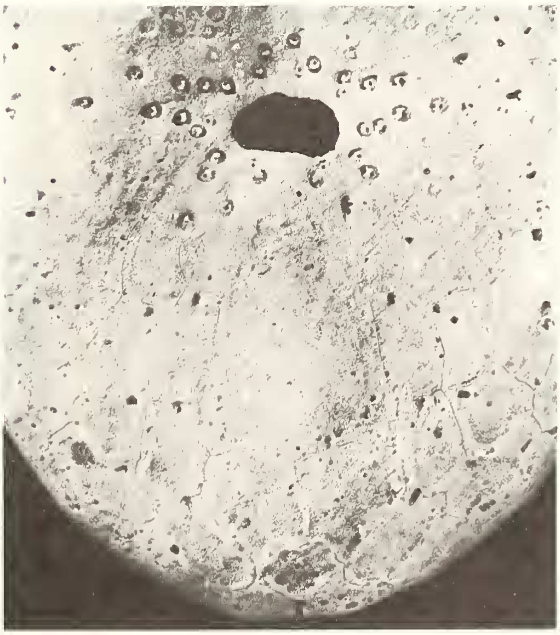

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FOSTER and PHILIP, Tertiary holasteroid echinoids

Cove, Glenaire (38° 48′ S., 143° 26′ E.) in the Otway Basin of Victoria and is of upper late Eocene age corresponding to P16 or P17 of the letter zonation. The earliest occurrence of the species in Australia is in the middle or lower late Eocene Wilson Bluff Limestone of the Eucla Basin (P14–15) and the last in the upper early Miocene Wataepoolan Limestone of the Otway Basin (N8).

In New Zealand a single crushed *Corystus* (BM E16517), which could represent this species, occurs in the early Oligocene (Whaingaroan) Cobden Limestone at Greymouth, corresponding to P19. However, undoubted specimens occur higher in the Cobden Limestone in the late Oligocene (Duntroonian–Waitakian) in P20–22 (Perpendicular Point S37/f620, 732–734; specimens NZGS EC561, 562, 564, 565, and OU8583h). The species also occurs at the base of an unnamed limestone of the same age on the Seymour River, near the junction with the Clarence (locality S41/f542; NZGS EC367–371). The last occurrences are in the late Oligocene or early Miocene (Waitakian–Otaian) Gee Greensand in the range P21–N4 (Gee's Point S136/f901, 1222; specimens NZGS EC823–826, and OU6631, 6632), and in the early Miocene (Otaian) Mahoenui Group in N4 (Hangatikei N83/f539; specimen E260 from Auckland University).

Measurements. Foster and Philip (1976*b*) give measurements of Australian material. The only well-preserved specimen from New Zealand (NZGS EC824) is 48 mm long, 46 mm wide, and 28 mm high.

Description. Test ovoid with a slight to almost imperceptible anterior notch. Upper surface gently domed and sloping to ambitus. Lower surface slightly sunken around the peristome; keeled plastron produced into an anal rostrum which is often quite pronounced.

Apical system often slightly sunken, located in front of centre, disjunct, with four genital pores. Ambulacra all similar, subpetaloid, and not constricted distally. Pore-pairs decrease in size towards the ambitus and continue on to the lower surface to the prominent phyllodes which consist of enlarged, deeply countersunk pore-pairs. In a minority of specimens the proximal ends of ambulacra I and V curve backwards as they approach the oculars. Ambital plates of the paired ambulacra low and geniculate.

Transverse-oval periproct situated above anal rostrum at termination of posterior slope. Transverse-oval peristome placed in a shallow depression a little in front of centre; the posterior margin is not labiate.

Upper surface finely granulate with scattered small tubercles which increase in size and density towards the ambitus. Oral surface densely covered with small perforate crenulate tubercles except for the finely granulated areas of the phyllodes and ambulacra I and V. An additional broad granulated area extends from the subanal fasciole to the periproct, and is bounded laterally by the proximal pore-pairs of ambulacra I and V and carries a few scattered tubercles. Tubercles are often absent from the tip of the subanal rostrum, which is instead finely granulated (Pl. 86, fig. 5).

Labrum broad, extending half way along the length of the second adjacent ambulacral plate, making wide contact with the shield-shaped sternal which extends to the middle of the fourth adjoining ambulacral plate. Sternal followed by a symmetrical pair of episternal plates, followed by a single small plate which corresponds to the snout of the subanal rostrum. The rostral plate abuts the fifth ambulacral plate on each side. Then follow three pairs of alternating pre-anal plates, the last of which forms the adoral margin of the periproct. In interambulacra 1 to 4 each primordial plate abuts against two succeeding plates in the amphiplacous manner.

Subanal fasciole roughly oval, encircling the rostral plate. There are no pore-pairs within the fasciole. Posterior segment of the fasciole is difficult to identify as the granules merge into those of the granulated area beneath the periproct.

EXPLANATION OF PLATE 86

Figs. 1–5. *Corystus dyasteroides* (Duncan). 1, lateral view of NZGS EC824, Gees Point, Gee Greensand, New Zealand, ×1. 2, lateral view of SAM P18013, a particularly high-tested specimen, Wool Bay, Yorke Peninsula, South Australia, ×1. 3, enlargement of the sunken peristomial region of NMV P19991, showing the countersunk pore-pairs of the phyllodes, Waurn Ponds, Victoria, ×3 approx. 4, posterior view of NMV P19993 showing rounded peristome with the closely granulated area beneath, Waurn Ponds, Victoria, ×2. 5, plastron and rostrum of NMV P19991, Waurn Ponds, Victoria; note the subanal fasciole and granulated rostrum, ×3.

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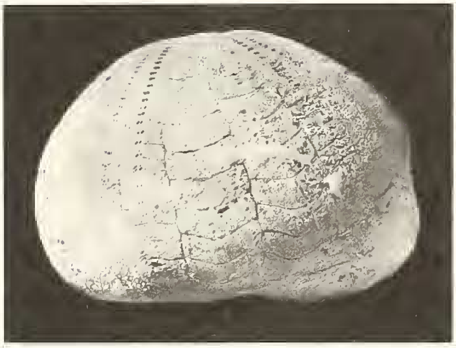

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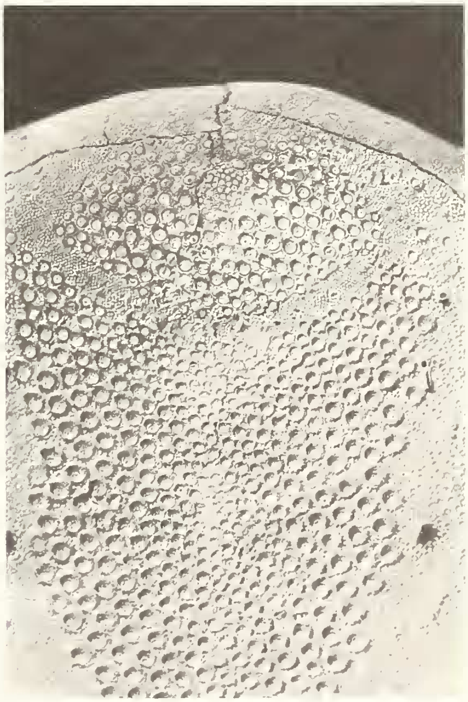

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FOSTER and PHILIP, Tertiary holasteroid echinoids

Remarks. Though never abundant, this distinctive species is widely distributed through the mid Tertiary of Australia, and is one of the most characteristic members of the fauna. Judging from the available material, it is not so common in New Zealand. It is found most often in the bryozoal lime grainstones so prevalent in the Tertiary of south-eastern Australia, and therefore it presumably lived in a shallow, relatively high-energy environment. The animal's stout test tends to substantiate this deduction.

Corystus dysasteroides is one of the few documented continuous evolutionary lineages among echinoids. Foster and Philip (1976*b*) subjected samples representing seven populations from the late Eocene to early Miocene to statistical analysis. The individuals that comprised those samples appear to get larger with time, and both wider and higher relative to their length. The apical system has a stronger tendency to be sunken in individuals from the stratigraphically younger samples.

Genus CARDABIA gen. nov.

Name. From Cardabia Creek, Carnarvon Basin, Western Australia. The name is pronounced 'card-ah-buyer', with emphasis on 'buy'.

Type species. *Cardabia bullarensis* sp. nov.

Diagnosis. Small corystids lacking a frontal notch and with a flat upper surface relatively densely tuberculated. There are three genital pores.

Remarks. This new genus is clearly related to *Corystus* through the presence of a rostral plate. However, the earlier *Cardabia*, with three genital pores, can hardly have given rise to *Corystus* with four. As *Cardabia* had populated the Australian north-west coast in the Palaeocene before the opening of the seaway between Australia and Antarctica, their common ancestor must be sought in the pre-Palaeocene Indian Ocean.

Cardabia bullarensis sp. nov.

Plate 90, figs. 3, 4; Plate 91, figs. 1-3

Material and occurrence. Twenty-three specimens from the northern end of Giralia Anticline, Carnarvon Basin on Giralia Station, North West Division, Western Australia. Nine, including the holotype (WAM 73.361) and two paratypes (WAM 73.365, 73.366) are from the south side of the Bullara-Giralia road in the vicinity of the turn-off to Jubilee Bore at approximately 22° 40′ S., 114° 13′ E., and about 6·5 km south of the bore. Although the echinoids were not found *in situ* they have traces of white glauconitic lime mudstone adhering to them. Eleven reddish silicified specimens were found loose 400 m south of a white hill about 5 km south of Jubilee Bore at approximately 22° 39′ S., 114° 14′ E. NMV P31199 was collected by T. A. Darragh and labelled 'Wadera Calcarenite, float on E. side of Main N.-S. tract of C-Y Creek (due E. of bore and E. of fence, Open Country Paddock), Yanrey 188147', at approximately 22° 52′ S., 114° 7′ E. A further two crushed echinoids (P31227, 31228) are probably the same species. They are from the type section of the Wadera Calcarenite, Old Marilla Station at 22° 50′ S., 114° 8′ E.

The Wadera, Pirie, and Cashin Calcarenites make up the Cardabia Group, and are of Palaeocene age (McWhae *et al*. 1958, p. 121). P. G. Quilty (pers. comm.) places the Cardabia Group outcrop in P4 and perhaps P5 and thus in the middle or late Palaeocene. From existing information it appears that the species is confined to the Cardabia Group and hence to the Palaeocene.

Measurements. The dimensions of the holotype are: length 20 mm, width 17 mm, height 10 mm. Other specimens from the same locality range from 14 × 11 × 8 mm up to 25 × 21 × 11 mm.

Description. Adapical and adoral surfaces flattened, with the ambitus uniformly rounded. Prominent plastronal keel which terminates in a slight anal rostrum; anterior margin gently rounded at the ambitus.

Apical system in front of centre, disjunct, with three genital pores; that of the madreporite is lacking. Ambulacra composed of small pore-pairs not easily discernible in unweathered specimens. Adapically the small round pores are placed close together and separated by a granule. The pore-pairs in the paired ambulacra placed slightly en-chevron; in ambulacrum III they are almost longitudinally directed.

Transversely oval periproct located just above anal rostrum. Subcircular, anteriorly located peristome with prominent phyllodes composed of deeply countersunk pores. Test coated with coarse granules and relatively dense small primary tubercles. Adoral surface with dense plastronal tuberculation but tubercles absent in the phyllodes and ambulacra I and V.

Plastronal plating consisting of a relatively long labrum extending to the second ambulacral plate, followed by a single large sternal plate extending to the fourth ambulacral plate. There follows a pair of episternal plates (the suture which separates them is only discernible with difficulty in the available material). The episternals are succeeded by a single plate, in the position of the point of the rostrum, and then two pairs of pre-anals. A subcircular subanal fasciole encloses the rostral plate.

Remarks. This new species is readily distinguished from specimens of *Corystus dysasteroides* in the Australian Tertiary by its smaller size, three genital pores, flat upper and lower surfaces, less prominent pore-pairs arranged en-chevron, subcircular peristome, coarser and more dense tuberculation, and the absence of a frontal notch.

Genus HUTTONECHINUS gen. nov.

Name. After Capt. W. H. Hutton who described the type species.

Type species. Macropneustes spatangiformis Hutton, 1873.

Diagnosis. Large, domed corystids, lacking an anterior notch, but with a wide, deep ambulacral groove running from the anterior margin to the peristome. Disjunct apical system with four genital pores. Ambulacra all similar, flush with the test and straight, expanding uniformly to the ambitus. Periproct transversely elongate, barely supra-marginal. Peristome rounded and facing forwards at the termination of the anterior groove. Posterior paired interambulacra strongly meridoplacous. Labrum long and narrow, its extremity abutting against the narrow sternal which with the large expisternals forms a plastronal keel. Small rostral plate surrounded by a subanal fasciole.

Remarks. This genus is again monotypic. Although the disposition of plastronal plates in relation to adjacent ambulacral plates is the same as *C. dysasteroides*, both the labrum and sternum are much longer and much narrower. The proportions of the episternals and rostral plate also differ markedly. In addition, *Huttonechinus spatangiformis* differs in its more simple ambulacra, its deep, broad, anterior ambulacral groove and in the posterior paired interambulacra, which are meridoplacous. These features, together with the absence of an anterior notch, warrant its separation from *Corystus*, to which genus the species was referred by Eames (1968).

The genus is known only from the Oligocene Cobden Limestone of New Zealand. This is a marly lime mudstone with its echinoid fauna dominated by large, thin-tested irregular echinoids. These, plus the fine-grained sediment, suggest that the habitat of *Huttonechinus* was relatively deep, quiet water. Similar lithologies are not represented in Oligocene outcrops in the south-eastern part of Australia, which may explain the absence of *Huttonechinus* from the Australian record.

Huttonechinus spatangiformis (Hutton, 1873)

Plate 87, figs. 1-4; Plate 88, figs. 1-3; text-fig. 2

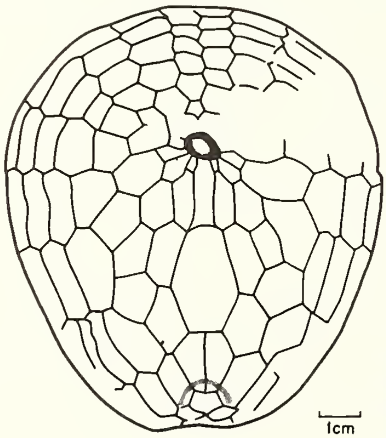
1870 *Macropneustes spatangiformis* Hector, p. 192 (*nomen nudum* text-fig.).
1873 *Macropneustes spatangiformis* Hutton, p. 40.
1887 *Holaster spatangiformis* (Hutton); Hutton, p. 268.
1894 *Holaster spatangiformis* (Hutton); Tate, p. 123.
1968 *Duncaniaster spatangiformis* (Hutton); Eames, p. 367.

Material and occurrence. This species appears to be common in the Cobden Limestone at Greymouth on the west coast of the South Island of New Zealand, 42° 21′ S., 171° 13′ E.; the age is Whaingaroan (early Oligocene) corresponding to P19. From here are the holotype NZGS EC831, and further specimens EC772, 780, 786, 787, 789, 791, 794, 801, 804-807, 809, 811-813, localities for these are numbered S44/f465, 469, 476, 490, 619; specimens 44, 47 in Canterbury Museum are also from this area. A further series of poorly preserved large holasteroid echinoids from the same place (BM E16507-16512, 16517) apparently represent the same species.

Measurements. All available specimens are crushed, and no accurate measurements are possible. Dimensions of the holotype are: length 99 mm; width 82 mm; height 43 mm; the largest specimen has a length of 110 mm.

Description. Adapical surface smoothly domed, with flat adoral surface apart from a plastronal keel and a deep anterior groove running from anterior margin to peristome. Ambital outline smoothly rounded with greatest transverse diameter in front of centre.

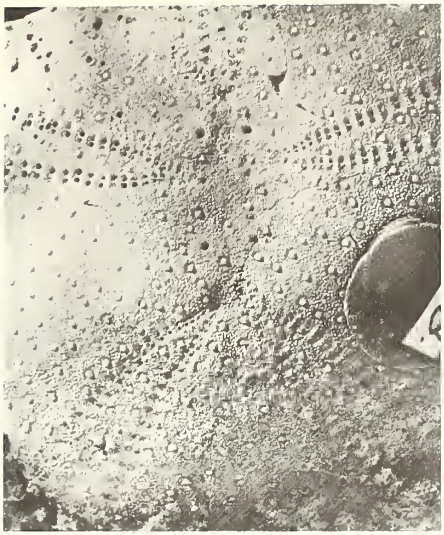
Apical system at summit of domed upper surface; disjunct, with four genital pores. Ambulacra straight, expanding uniformly from apex to ambitus, with small circular pores diminishing markedly in size towards ambitus. Adapical pore-pairs slightly sunken and transverse in the paired ambulacra, and en-chevron in



TEXT-FIG. 2. *Huttonechinus spatangiformis* (Hutton). Plating of adoral surface of NZGS EC805; subanal fasciole from NZGS EC811.

EXPLANATION OF PLATE 87

Figs. 1-4. *Huttonechinus spatangiformis* (Hutton). 1, apical system, NZGS EC794, ×2. 2, posterior termination of adoral surface of NZGS EC772 showing periproct; the shield-shaped plate at the posterior end of the plastron in fact consists of the two episternals and the small central rostral plate, ×2. 3, adapical view of holotype, NZGS E831, ×1. 4, enlargement of apical system of holotype, ×2. All specimens from the Cobden Limestone, Greymouth, New Zealand.



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FOSTER and PHILIP, Tertiary holasteroid echinoids

ambulacrum III. Several enlarged pore-pairs around the peristome form the phyllode. Periproct transversely elongate, barely supramarginal, and occupying most of the small posterior truncation. Anal rostrum slightly developed or absent. Subcircular peristome facing forwards at the termination of the deep anterior groove.

Test covered with fine granules, overlain by uniform, sparsely distributed tiny tubercles which become slightly larger and more closely spaced towards and on the adoral surface; only on the plastron is the tuberculation reasonably dense. The labrum is long and narrow but broadens posteriorly to abut against the relatively long and narrow sternum. The pair of symmetrical episternals form a hexagon and are followed by a small, transversely elongate rostral plate which occupies the break of slope between the adoral surface and the subanal truncation. Labrum and succeeding plastronal plates form a narrow keel. Interambulacra 1 and 4 strongly meridoplacous. A subanal fasciole appears to encircle the rostral plate.

Remarks. Because of the fragmentary nature of the available material, a number of specimens have been used to build up the above description of the species (in particular EC772, 780, 794, 804, 806, 811).

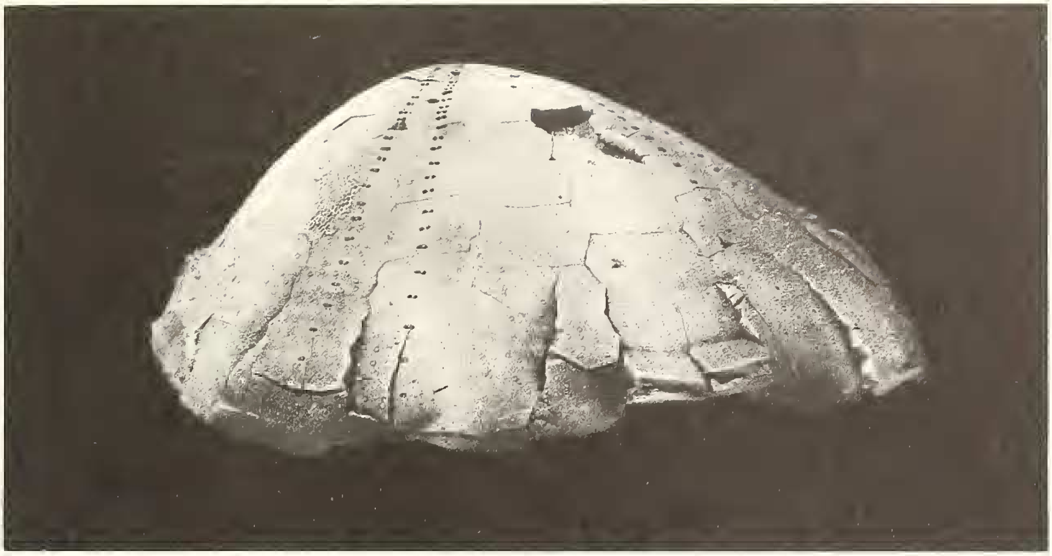
Two specimens in the suite of material from the Cobden Limestone appear to have characters outside those here understood for *Huttonechinus spatangiformis*. One smaller specimen (BM E16513), although badly crushed, exhibits a pronounced anal rostrum and an anterior notch and so is here referred to *C. dysasteroides*. Another larger specimen, number 36 from Canterbury Museum and again badly crushed, has a vertically elongate periproct and a pronounced subanal sulcus running to the rostral plate; an old label names it as '*Holaster cordatus*'.

Hector (1870, p. 192) published the two names *Macropneustes spatangiformis* and *M. cordatus* without description. Hutton (1873) briefly described both, together with a third, *M. australis*. Subsequently Hutton (1887, p. 268) removed *spatangiformis* and *cordatus* to *Holaster*, with which Tate (1894, p. 123) concurred. Mr. I. W. Keyes, Technical Officer of the New Zealand Geological Survey (pers. comm.), holds that the types of *cordatus* and *australis* no longer exist. Tate described the holotype of *H. cordatus* as follows: 'the type is incomplete in the anal region, but is higher than *H. australiae* Duncan, and has nearly equal basal diameters'. Specimen 36 (mentioned above) is certainly not the missing holotype, and whether it is correctly referred to *H. cordatus* cannot be determined; it is too poorly preserved to warrant description. Tate (1894, p. 124) wrote that the holotype of *M. australis* 'is founded on a fragment of a large spatangoid without ambulacra, vent, vertex or peristome. No useful purpose can be served by its retention.' The same can be said also of *H. cordatus*, so that both are here regarded as *nomina dubia*.

Fell (1953, p. 246) recorded the genus *Echinocorys* from the Oligocene of New Zealand. The material of *H. spatangiformis* in the British Museum (Natural History) has with it a note by L. Bairstow 'Determined by H. B. Fell 21.12.53 as: probably *Echinocorys*, though '*Holaster spatangiformis* Hutton'; basal Oligocene, Whaingaroan stage, Cobden Limestone, Point Elizabeth, Greymouth, the type locality of '*H. spatangiformis* Hutton'. Eames (1968, p. 367) referred the material to *Duncaniaster* (now *Corystus*). The record of *Echinocorys* in New Zealand has yet to be substantiated.

EXPLANATION OF PLATE 88

Figs. 1-3. *Huttonechinus spatangiformis* (Hutton). 1, lateral view of NZGS EC806, ×1. 2, adoral view of NZGS EC805, showing broad anterior ambulacral groove, ×1. 3, adapical view of NZGS EC806, ×1. Both specimens from the Cobden Limestone, Greymouth, New Zealand.



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FOSTER and PHILIP, Tertiary holasteroid echinoids

Family HOLASTERIDAE Pictet, 1857
Genus GIRALIASTER gen. nov.

Name. From the Giralia Range, Carnarvon Basin, Western Australia.

Type species. *Giraliaster jubileensis* sp. nov.

Diagnosis. Medium to large holasterids approximately as broad as long, with a pronounced anterior sulcus that deeply notches the ambitus and continues to the anteriorly placed ovate peristome. Apical system subcentral, disjunct with four genital pores. The longitudinal-oval periproct is placed vertically on the posterior truncation. Plastron keeled.

Pores of the anterior ambulacrum are very small and separated by a granule. Paired ambulacra are flush with the test, subpetaloid, with extremities not constricted. Posterior pore fields of each petal with large, elongate, conjugate pores, in contrast to the smaller, round, and non-conjugate, or subconjugate pores of the anterior pore fields. Anterior petals distinctly longer than posterior. Posterior ambulacra with single pores from just above the ambitus to the extremities of the phyllodes.

Adapical surface finely and sparsely granulate with comparatively large perforate, crenulate tubercles along raised margins of anterior sulcus and extending on to adoral surface. Subanal fasciole broad and bilobed.

Distribution. *Giraliaster* first appears in the late Cretaceous Miria Marl of the Carnarvon Basin, Western Australia, and apparently reached New Zealand as early as the late Palaeocene or early Eocene (P6–7). It occurs in the middle and late Eocene of the Australian south coast (P14 or P15 to not later than the P15/16 boundary); and lingers on, in New Zealand only, at least to the late Oligocene (P21–22).

Remarks. *Giraliaster* is a typical holasteroid except that portions of the posterior ambulacra carry but single pores; it corresponds closely in most respects to *Cardiaster*. However, it lacks the characteristic marginal fasciole of *Cardiaster* and has instead a subanal fasciole. Although Mortensen (1950, p. 43) in general places no great classificatory value on fascioles among holasteroids, they are certainly not an evanescent feature in the Cainozoic forms described here.

The holasteroid genera *Basseaster*, *Garumnaster*, *Stereopneustes*, and *Corystus* have a subanal fasciole; but in their other characteristics all are well separated from *Giraliaster*. In *Basseaster* from the Maastrichtian of Madagascar, *Garumnaster* from the Danian of Europe, and *Corystus* from Australasia the ambulacra are not petaloid, the frontal notch is absent or only weakly developed, and an anal rostrum is present. *Stereopneustes* is a living Indo-Pacific genus without a frontal notch but with subpetaloid ambulacra; however, the pores in the petals are neither elongate nor conjugate.

Single pores in the ambulacra appear to be a modification of an original biporous condition, and are normally present in the specialized families Pourtalesiidae, Calymnidae, and Urechinidae. In the Holasteridae, *Basseaster* may have single pores in the anterior ambulacrum but retains double pores elsewhere.

The various species of *Giraliaster* are distinguished by differences in the shape of the test, and different numbers of pore-pairs in the proximal parts of the ambulacral petals. In all species, the distal part of each petal is marked by the inflection of the outer ambulacral sutures toward the interambulacra so that the pore-pairs thereafter are more centrally located on each plate (text-fig. 4). The number of pore-pairs to this inflection point in each petal is given for the available material in Table 1.

Giraliaster jubileensis sp. nov.

Plate 89, figs. 1–6; text-figs. 3, 4*a*

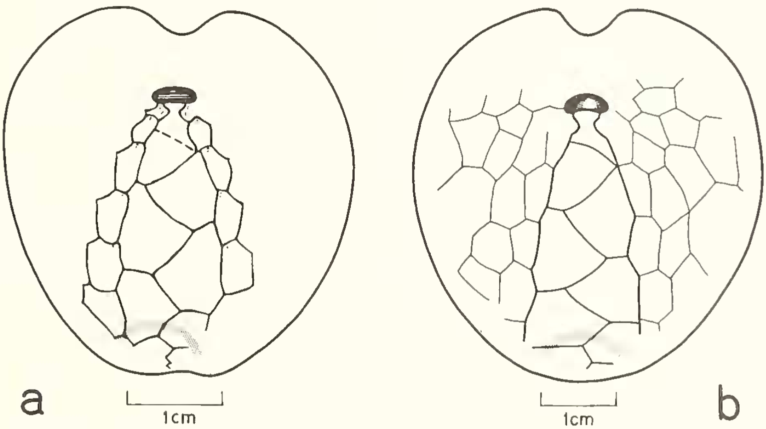
1956 *Cardiaster* spp. Brunnschweiler *in* Condon *et al.*, pp. 32, 37, 40.

Diagnosis. A comparatively small species of *Giraliaster* with a steep anterior slope and an abrupt posterior truncation. Apical system slightly in front of centre. Adapical ambulacra subpetaloid with posterior pore fields of paired ambulacra with slightly elongate and weakly conjugate pores.

Material and occurrence. This species is the most abundant echinoid in the middle or late Palaeocene Cardabia Group of the Carnarvon Basin, north-west Western Australia (Condon *et al.* 1956). In the collections made by Condon *et al.* it occurs first in the Maastrichtian Miria Marl at Learmonth (CPC F21702), in the Wadera Calcarenite, and is most abundant in the overlying Pirie Calcarenite; however, it also extends up through the Cashin and Jubilee Calcarenites. The youngest occurrence is among reworked echinoids (CPC F21680) from the base of the Giralia Limestone (Middle Eocene) in the Giralia Range. Altogether some 130 specimens are present in the material collected by Condon *et al.* The species is identified as *Cardiaster* spp. in their stratigraphic sections. Most of the material is, however, poorly preserved, being often crushed and desert weathered.

In addition, twenty-three specimens are available from the northern end of the Giralia anticline from the vicinity of Jubilee Bore. Seventeen, including the holotype WAM 73.362 and paratypes WAM 73.363 and 73.364 are from the lower slopes of a white hill 4·5 km south-east of Jubilee Bore (approximately 22° 39½′ S., 114° 14½′ E.). The others are from a ridge 500 m south of the Giralia–Bullara road south of Jubilee Bore (approximately 22° 40½′ S., 114° 13′ E.). The parent formation of these collections could not be identified with assurance.

Description. Test cordate, with moderately deep anterior groove running from apical system to peristome. Upper surface arched, sloping abruptly to anterior margin and more gently to top of posterior truncation. Lower surface flat except for keeled plastron and sunken area in front of peristome.



TEXT-FIG. 3. *Giraliaster jubileensis* gen. et sp. nov. *a*, platronal plating of WAM 73.363. *b*, plastronal plating of CPC F21725.

TABLE 1. Measurements of different species of *Giraliaster*.

	Dimensions (mm)			Proportions* (%)		Number of pore-pairs			
	l	w	h	height	apical system	Anterior II	IV	Posterior I	V
Giraliaster jubileensis sp. nov.									
WAM 73.364	46	47	30	65	42	21	23	17	16
holotype	46	41	24	52	45	17	19	—	—
NZGS EC417	44	44	31	70	48	17	—	12	—
—	40	37	30	75	40	20	20	13	14
—	39	39	25	64	45	—	17	11	12
—	38	39	20	53	43	—	18	—	11
G. tertiarius (Gregory)									
—	?	60	37	—	—	26	—	—	—
—	60	58	36	60	48	28	—	—	—
Brighton (N.Z.)	55	53	35	64	57	—	27	18	—
SAM P18014	54	52	32	59	48	31	33	19	19
—	?	45	28	—	—	27	—	14	—
SAM P18015	47	44	28	60	47	25	26	14	14
—	46	44	29	63	50	26	—	16	—
—	?	44	30	—	—	—	27	—	15
holotype	42	41	25	60	56	25	—	16	—
G. sulcatus (Hutton)									
NZGS EC827	98	101	37	38	68	36	—	21	—
SAM T286	84	87	35	42	63	33	32	16	17
holotype	67	73	23	34	57	—	30	—	18
G. bellissae sp. nov.									
Wilson Bluff	95	90	42	47	52	—	35	16	15
holotype	94	88	51	54	54	26	26	15	15
Tortachilla	79	75	39	49	53	—	31	15	—

* Proportions: height as a percentage of length, and distance to centre of apical system from anterior margin as a percentage of length.

Apical system disjunct with four genital pores present. Pore-pairs of ambulacrum III very small, with outer pore uppermost. Pores in each pair separated by a granule.

Paired ambulacra subpetaloid with the anterior pair the longer. Petals not closed but pore-pairs becoming further apart, and pores becoming gradually smaller towards the ambitus. Anterior pore fields of ambulacra II and IV comprise small round pores in each pair separated by a granule; posterior pore fields of slightly larger, somewhat elongate pores, with pore-pairs weakly conjugate in the central portion of the petal. Pores in ambulacra I and V smaller than in anterior paired ambulacra, although the posterior pore fields are similar.

EXPLANATION OF PLATE 89

Figs. ×1 unless otherwise stated.

Figs. 1–6. *Giraliaster jubileensis* gen. et sp. nov. 1, adapical. 2, adoral. 5, lateral view of holotype, WAM 73.362. 3, adoral view of paratype, WAM 73.363. 4, adapical view of paratype, WAM 73.364. All specimens, 4·5 km south-east of Jubilee bore, Carnarvon Basin. 6, enlargement of surface of paratype, CPC F4821 (*ex* F21708), Pirie Calcarenite, northern part of Giralia Anticline, Carnarvon Basin, ×4.

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The termination of the petaloid area of the ambulacra is marked by a sudden increase in the width and height of the ambulacral plates. As a consequence the pore-pairs move out from the adradial suture, and there is a greater distance between succeeding pore-pairs. The pores become gradually smaller and less elongate as the pairs become further apart.

In ambulacra II and IV there is an abrupt transformation a short distance above the ambitus to very small round pores separated by a granule. At the ambitus, the pores of a pair become oblique to the direction of the ambulacrum and, on reaching the adoral surface, they complete their rotation to be one above the other, and so continue to the prominent phyllodes. Details of ambulacra I and V are not clear in the available material, but, on the adoral surface, the first three ambulacral plates posterior of the double-pored phyllodes carry a single minute pore.

Tuberculation of adoral surface inconspicuous except for somewhat larger tubercles along margins of anterior groove. Periproct comparatively large, oval, vertically elongate, placed at top of posterior truncation, with a vertically elongate depression immediately below it in most specimens. Small, oval peristome towards the anterior margin and at termination of anterior ambulacral groove.

Interambulacra 2, 3, and 4 with primordial plates at the peristome edge adjoining two plates in the next row. In interambulacrum 1 there is a single plate in the second row from the peristome, and it is this plate which adjoins two succeeding plates.

Plastron meridosternous (text-fig. 3). Subsequent plates form an alternating double series. The mid point of each plate, other than the labrum, is raised so that a ragged line of five nodes extends down the keeled plastron to the vicinity of the broad subanal fasciole.

Remarks. A single poorly preserved but uncrushed specimen from New Zealand (NZGS EC417, locality unknown) resembles *jubileensis* in gross features and is labelled '*Cardiaster brightoni* n. sp. holotype'. That it is not close to Brighton's (1929, p. 315) specimen is indicated by the smaller number of pores in its petals (see Table 1).

Giraliaster tertiarius (Gregory, 1890)

Plate 90, figs. 1, 2; Plate 92, figs. 2, 4, 5, 7; Plate 93, fig. 1; text-fig. 4*b*

1890 *Cardiaster tertiarius* Gregory, p. 484, pl. 14, figs. 2, 3.
1891 *Cardiaster tertiarius* Gregory; Tate, p. 277.
1892 *Cardiaster tertiarius* Gregory; Bittner, p. 360.
1924 *Holaster tertiarius* (Gregory); Lambert and Thiéry, p. 402.
1929 '*Cardiaster*' *tertiarius* Gregory; Brighton, p. 317, fig. 18*a*, *b*.
1929 '*Cardiaster*' sp. nov. Brighton, p. 315, figs. 14–17.
1946 *Cardiaster tertiarius* Gregory; Clark, p. 360.
1970 '*Cardiaster*' *tertiarius* Gregory; Philip, p. 183.

Diagnosis. A medium-sized species of *Giraliaster* with a central apical system and a gently arched upper surface. Adapical ambulacra subpetaloid with the posterior pore fields of paired ambulacra with elongate and conjugate pores.

EXPLANATION OF PLATE 90

Figs. 1, 2. *Giraliaster tertiarius* (Gregory). 1, apical system of SAM P18015, ×3. 2, apical system of SAM P18017 (*ex* AUGD F15772), ×3. Both specimens from Maslins Beach, Gulf St. Vincent, South Australia.

Figs. 3, 4. *Cardabia bullarensis* gen. et sp. nov. 3, enlargement of adapical surface of paratype WAM 73.365, showing the three genital pores and the simple pore-pairs in ambulacrum I, ×4 approx. 4, enlargement of adoral surface of paratype WAM 73.366, showing the phyllode and some of the sutures, ×4. Both specimens from north end of Giralia Anticline, Carnarvon Basin, Western Australia.

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Material and occurrence. Gregory's holotype (BM E3382) is from 'Willunga', and there is little doubt that it is from the Tortachilla Limestones (Reynolds 1963, p. 123) at Maslins Beach just north of Port Willunga on the eastern shore of Gulf St. Vincent. A further ten specimens, of which only SAM P18014, 18015 are relatively complete, are available from the Tortachilla at Maslins and Christies Beaches. Most, and perhaps all, the specimens come from the upper Glauconitic Limestone Member of Reynolds (1963, p. 124) whose age is early late Eocene in upper P15 (McGowran *et al.* 1971, fig. 14-1). A New Zealand occurrence is discussed below.

Description. Test cordate, with moderately deep anterior groove running from apical system to peristome. Upper surface gently arched, sloping evenly to margin of test except at the posterior truncation. Lower surface gently curved from margin of test to broadly keeled plastron; area in front of peristome sunken.

Tuberculation, periproct, peristome, apical system, and details of ambulacrum III are as in the type species.

Paired ambulacra petaloid, with the anterior pair much the longer. Petals not closed but pore-pairs become further apart, and pores become gradually smaller, towards the ambitus.

Anterior pore fields of ambulacra II and IV with small, slightly elongate pores, close together and with the pairs slightly conjugate. In the posterior pore fields the pores are larger, more strongly elongate and further apart, with the pore-pairs distinctly conjugate. Posterior pore fields of ambulacra I and V have larger and more elongate pores in more strongly conjugate pairs than the anterior pore fields. However, the contrast is not as great as in the anterior paired ambulácra.

The termination of the petaloid area of the paired ambulacra is marked by an abrupt increase in the width and height of the ambulacral plates which is not matched by any immediate reduction in size of the pores. Beyond the petaloid area of ambulacra II and IV, the configuration of the pore-pairs is the same as in the type species. In ambulacra I and V the pores gradually diminish in size approaching the ambitus. Just below the level of the top of the periproct, the small double pores are replaced by minute single pores which continue on the lower surface to the double-pored phyllodes. The rounded subanal fasciole encompasses part of three plates of ambulacra I and V, but in each case the pore is outside the fasciole.

Remarks. G. tertiarius differs in shape from *G. jubileensis* by having its apical system placed further back, with a less abrupt slope to the anterior margin. The ambulacra have larger and more elongate pores with the pore-pairs more strongly conjugate. There are relatively more pore-pairs in the petaloid part of the anterior paired ambulacra; and there is a greater contrast in length between the petaloid parts of the anterior and posterior paired ambulacra (see Table 1).

Brighton (1929, pp. 315–318, figs. 14–17) described as '*Cardiaster*?, sp. nov.' a single fragmentary *Giraliaster* from Chatham Islands, New Zealand, which he considered closely resembled '*Cardiaster*' *tertiarius* Gregory. The specimen is from the Red Bluff Tuff at the north end of Red Bluff, six miles north of Waitangi, and (I. W. Keyes, pers. comm.) is possibly from the Waipawan Stage of late Palaeocene–early Eocene age (corresponding to P6–7). The differences in shape and ambulacra which distinguish this specimen from the holotype fall within the range of *G. tertiarius* and the specimen is here referred to this species. The age of this occurrence should be substantiated by further material.

EXPLANATION OF PLATE 91

All figs. ×1.

Figs. 1–3. *Cardabia bullarensis* gen. et sp. nov. Adapical, lateral, and adoral views of holotype, WAM 73.361, north end of Giralia Anticline, Carnarvon Basin, Western Australia.

Figs. 4–6. *Giraliaster bellissae* sp. nov. Lateral, adapical, and adoral views of holotype, NZGS E849, Awamoko Creek, North Otago, New Zealand.


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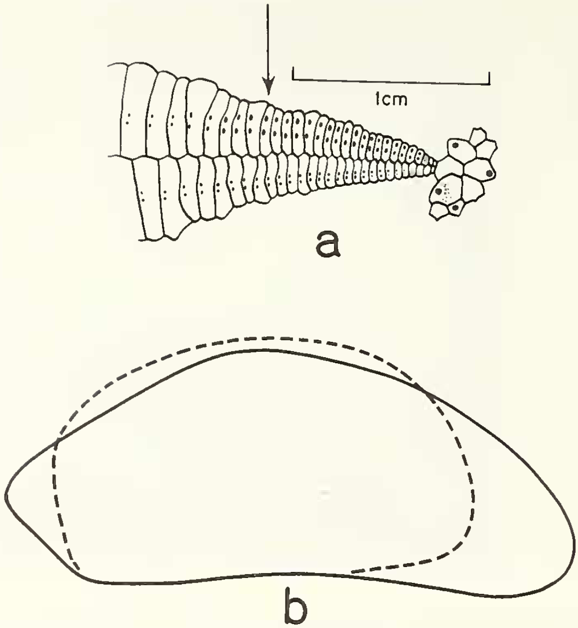


TEXT-FIG. 4. *Giraliaster* spp. *a*, *G. jubileensis*, plating of ambulacrum II of WAM 73.364, showing inflection point of the pore-pairs. *b*, profiles of *G. sulcatus* (Hutton) and *G. tertiarius* (Gregory) (broken line).

Giraliaster sulcatus (Hutton, 1873)

Plate 93, figs. 3, 5; text-fig. 4*b*

1873 *Amphidotus sulcatus* Hutton, p. 41.
1891 *Cardiaster latecordatus* Tate, p. 281.
1894 *Cardiaster sulcatus* (Hutton); Tate, p. 124.
1946 *Cardiaster latecordatus* Tate; Clark, p. 361.
1970 '*Cardiaster*' *latecordatus* Tate; Philip, p. 183.

Diagnosis. A large flat species of *Giraliaster* with a posteriorly placed apical system. Adapical ambulacra subpetaloid; posterior pore fields of paired ambulacra with strongly elongate and conjugate pores.

Material and occurrence. Hutton's holotype (NZGS EC690) is a flattened, slightly telescoped, and incomplete specimen from 'Oamaru', New Zealand. A. R. Edwards (pers. comm.) identified the matrix of the specimen as typical of the finer-grained parts of the Totara and McDonald Limestones, and puts the age at late Kaiatan to earliest Whaingaroan on the basis of the calcareous nannofossil assemblage. Thus the age is in the range mid late Eocene to basal Oligocene or P15–18. Additional New Zealand material, none of it well preserved, referable to this species is: NZGS EC567 from locality S37/f618 on the coast 8·5 miles south of Fox River, of questionable Runangan age (late Eocene or uppermost P15–17); NZGS EC827 from S136 at Taylor's Quarry, Oamaru, of early Whaingaroan age (very early Oligocene or P18–19); NZGS EC820 from S37/f617 near algal band, on coast opposite Seal Island 1 mile south of Fox River, of Whaingaroan to Duntroonian age (early or mid Oligocene or P18–21).

In Australia the species is represented by SAM T286, the holotype of *Cardiaster latecordatus* whose locality Tate (1891, p. 281) gives as 'Glauconitic limestone, Aldinga Cliffs'. This could refer to either the

Glauconitic Limestone Member of the Tortachilla Limestone or the overlying Blanche Point Transitional Marls (Reynolds 1953, p. 125) at Maslins Beach, south of Adelaide. However, the appearance of the specimen suggests that it came from the glauconite basal Transitional Marl Member of the overlying Blanche Point Marl. It is lower Upper Eocene in age, probably in P15 close to the P15–16 boundary.

Description. Test cordate, with moderately deep anterior sulcus running from a point some distance in front of apical system to peristome; there are pronounced ridges on either side of the groove. Upper surface in the form of a rather flat cone culminating in front of the apical system. Anterior and lateral margins of the test sharp and posterior margin overhanging. The posterior margin particularly is crushed so that posterior truncation is not apparent. Lower surface flat with the exception of a transverse prominence below the periproct; this again may be exaggerated through distortion of the test.

Apical system and ambulacrum III as for the genus. The anterior groove begins abruptly some ten plates from the termination of the ambulacrum, measured down ambulacrum III*a* from the occular plate. Apical system situated towards the rear of the test.

Paired ambulacra subpetaloid, anterior pair much the larger. The posterior pore fields of the paired petals have strongly elongate pores, and the pairs are strongly conjugate. The pores of the anterior pore fields slightly elongate and distinctly conjugate. Pores of the anterior and posterior paired ambulacra similar.

Subanal fasciole present. Tuberculation of the upper surface very fine and relatively sparse. Only on the keeled edges of the anterior groove are there larger crenulate and perforate tubercles. Details of peristome, periproct, or tuberculation of the lower surface not known.

Remarks. Because of the poor preservation of the holotype the above description is based largely on the type specimen of Tate's *C. latecordatus* which, although slightly crushed, is complete and the adapical surface is well preserved. All the large, flat, Australasian *Giraliaster* specimens are here placed in a single variable species. Tate (1894, p. 124) had already recognized the likelihood that his *latecordatus* and Hutton's *sulcatus* are synonymous and despite the indifferent preservation of the type and the three-line original description, Hutton's name has precedence. Better material is needed before any separation could be justified.

G. sulcatus, although still rare, appears to be the most common species of *Giraliaster* in New Zealand. Its range is not yet well defined, with a first appearance in P15–17 and last occurrence in P18–21, corresponding to late Eocene to Oligocene. In Australia the species is apparently restricted to P15–16.

Tate's single specimen from Aldinga, S.A., differs from *G. tertiarius* (Gregory) (which is frequently encountered in the underlying Tortachilla Limestone at the same locality) in being larger and flatter; and in having a conical rather than evenly arched upper surface (see text-fig. 4*b*); and a sharp rather than smoothly rounded margin. The apical system is towards the posterior instead of being central.

Giraliaster bellissae sp. nov.

Plate 91, figs. 4–6

1970 '*Cardiaster*' *tertiarius* Gregory; Philip, pl. 5.

Diagnosis. A large and relatively high species of *Giraliaster* with a centrally placed apical system. Posterior pore fields of paired ambulacra with strongly elongate and conjugate pores.

Material and occurrence. The holotype is a reasonably well-preserved specimen (NZGS EC849) collected by Stella Belliss and P. A. Maxwell from the Prydes Gully Member of the Otekaike Limestone, right bank of tributary of Awamoko Creek, locality J41/f37 near Rams Head Homestead, North Otago, New Zealand. The age is Duntroonian–Waitakian, probably Waitakian (late Oligocene, probably P21–22).

Four fragmentary specimens, from the Wilson Bluff Limestone at the Bluff in far western South Australia are here referred to this species. Their age is middle or early late Eocene (P14–15). One specimen is complete enough to enable dimensions to be estimated (Table 1).

A single specimen from the Glauconitic Limestone Member of the Tortachilla Limestone at Maslins Beach, south of Adelaide, South Australia, is also questionably referred to this species. Its age is early late Eocene in upper P15. The specimen is in relatively good condition, but lacks the periproct and subanal area.

Description. Test circular in plan except for deep anterior notch and posterior prominence above periproct. In lateral view the anterior surface curves smoothly up to the highest point in front of the apical system which is situated on the long uniformly sloping posterior surface. The short posterior truncation is adorally directed. Ambitus curving smoothly to a rather flat adoral surface.

Apical system typical; ambulacra similar to *G. sulcatus.* Periproct large, circular, visible from below, occupying half of the height of the posterior truncation; a circular subanal fasciole present. Peristome transversely elongate, slightly labiate, visible from the front.

Remarks. This species is distinguished from *G. sulcatus* by its greater relative height and more centrally placed apical system. It differs from *G. tertiarius* and *G. jubileensis* in the steeper posterior slope of the adapical surface, the shorter and overhanging posterior truncation, and the much stronger conjugation of the pores in the anterior pore fields of the petals.

Philip (1970, pl. 5) identified a specimen from the Middle or Upper Eocene Wilson Bluff Limestone in the Western Australian part of the Eucla Basin in Weebubbie Cave as '*Cardiaster*' *tertiarius*, a species only previously recorded from the late Eocene Tortachilla Limestone of South Australia (Philip 1970, p. 183). Fragments of a large, relatively high, species of *Giraliaster* with a smoothly rounded ambitus are common in the Wilson Bluff Limestone at the Bluff; and this material is now identified as *G. bellissae.* The same identification is presumed to apply to the specimen from Weebubbie Cave. The species ranges from P14–15 up to P21–22.

Genus ECHINOCORYS Leske, 1778

1778 *Echinocorys* Leske, p. 175.
1950 *Echinocorys* Breynius; Mortensen, p. 378 (*cum synon*).
1953 *Echinocorys* Leske; Cooke, p. 24.
1959 *Echinocorys* Leske; Cooke, p. 66.

Type species. Echinocorys scutatus Leske, by monotypy.

Diagnosis. Moderate to large sized holasterids, elongate-oval in outline and lacking an anterior notch. Adapical surface hemispherical to domed; adoral surface flat. Peristome anterior, slightly reniform to oval; periproct inframarginal, usually elongately ovate. Ambulacra non-petaloid and similar, usually with rounded pores. Tubercles small and uniform.

Remarks. Stephenson (1963) has described a 'diffuse fasciole' encircling the periproct in the type species, and has drawn attention to Lambert's (1903) mention of a similar structure in other species of *Echinocorys.* The 'fasciole', however, is not well defined and is apparently variably developed, so that it is extremely doubtful whether any useful subdivision of the genus can be made on its occurrence. Although this surface detail of the available specimens of *E. australis* is not very well preserved, the new species apparently lacks such a structure.

Echinocorys is one of the most characteristic and prolific genera of the Upper Cretaceous of Europe. However, other Cainozoic records are known besides the present occurrence. *E. ovalis* (Clarke) (Cooke 1959, p. 66, pl. 27, figs. 6–9) comes from the Palaeocene of New Jersey, U.S.A. Fell's (1953, p. 246) record of the genus from the Lower Oligocene of New Zealand is apparently based on *Huttonechinus spatangiformis* (Hutton) (q.v.).

Echinocorys australis sp. nov.

Plate 92, figs. 1, 3, 6; Plate 93, figs. 2, 4; text-fig. 5

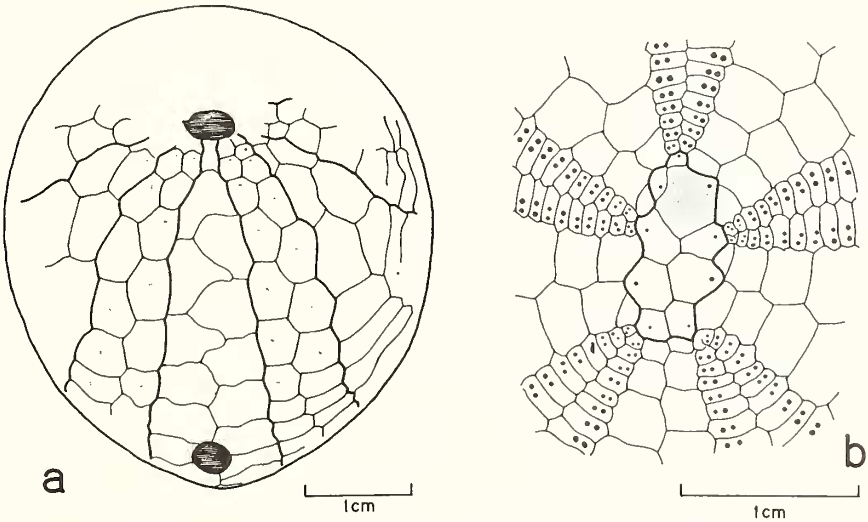
1956 *Echinocorys sulcatus* Goldfuss; Brunnschweiler *in* Condon *et al.*, p. 32.

Diagnosis. A comparatively small, low species of *Echinocorys* with a regularly domed adapical surface. Adapical pore-pairs small, closely spaced, and rounded. Genital 3 in apical system greatly reduced.

Material and occurrence. Holotype (CPC F4818) and two other specimens (F4819, F4820), from the basal half-metre thick, hard limestone at base of Wadera Calcarenite type section in Toothawarra Creek, 22° 49¾′ S., 114° 8½′ E., Carnarvon Basin, Western Australia. In addition WAM 72.424 was collected from spoil from the Wadera Calcarenite, 400 m north-west of Remarkable Hill, Cardabia Station. A larger specimen NMV P31200, also from the Wadera type locality, is here referred to the species. The age is middle or late Palaeocene.

Measurements

	length	width	height
CPC F4818	46 mm	41 mm	26 mm
CPC F4820	51 mm	44 mm	27 mm
WAM 72.424	64 mm	54 mm	28 mm
NMV P31200	75 mm	65 mm	38 mm



TEXT-FIG. 5. *Echinocorys australis* sp. nov. *a*, plastronal plating of holotype, CPC F4818. *b*, apical system of holotype.

Description. Test ovate in ambital outline, although the posterior is somewhat pointed. Lateral profile gently domed with greatest height just anterior of the apical system where the test is flattened. Adoral surface slightly concave, particularly around the distinctly sunken peristome. Plastron slightly raised above the neighbouring posterior paired ambulacra. Peristome transversely oval and located close to anterior margin. Periproct slightly ovate.

Apical system typically disjunct, with a greatly enlarged madreporite and a correspondingly reduced genital 3. Ambulacra straight with similar pore-pairs, except those of the posterior paired ambulacra which are reduced in size; phyllode also well developed. Ambulacral plates with centrally mounted non-conjugate pore-pairs. Pores similar and rounded.

Test covered with closely spaced granules and small, irregularly spaced perforate crenulate tubercles which are lacking on the plates of the posterior adoral ambulacra.

Remarks. Two of the available specimens have suffered fire damage. One of these (CPC F4819), although but a fragment, is illustrated for it shows well the plating structure near the ambitus. The peculiar double sutures no doubt are the result of differential calcining of growth rings within the plates. A similar effect may be caused by differential weathering.

In size and shape *E. australis* perhaps approaches most closely the late Cretaceous species *E. ciplyensis* Lambert (Smiser 1935, p. 45, fig. 24*a–c*) but it lacks the raised adoral ambulacra that characterize that species.

PALAEOGEOGRAPHIC CONCLUSIONS

The common occurrence of early Cainozoic holasteroid species in Australia and New Zealand bears on current palaeogeographic reconstructions. Text-fig. 6 shows the age and distribution of common species on the reconstruction for the opening of the Southern Ocean in the late Eocene (anomaly 19, 46 my) given by Deighton *et al.* (1976). Hayes and Ringis (1973, p. 454) found that sea-floor spreading in the central Tasman Sea ceased at 60 my, i.e. before the opening of the southern Australian seaway, and New Zealand is located accordingly in text-fig. 6.

It has been suggested above that the poorly known Maastrichtian form *Basseaster rostratus* Lambert from Madagascar may be a corystid. If this proves to be so, then the migration of the family to Australia is readily explained. Frakes and Kemp (1972, p. 98) have postulated an anticlockwise current in the Indian Ocean prior to the opening of the seaway between Antarctica and Australia, and such a current would facilitate migration of eastern African forms to the western Australian coast, especially those with long-lived larvae. There is some evidence of communication between the Australian and southern African echinoid fauna even after formation of

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EXPLANATION OF PLATE 92

All figs. × 1 unless otherwise stated.

Figs. 1, 3, 6. *Echinocorys australis* sp. nov. 1, lateral view of holotype, CPC F4818, Toothawarra Creek, Carnarvon Basin, Western Australia. 3, lateral view of fire-damaged specimen, CPC F4819, same locality, × 2. 6, adapical view of WAM 27.424, Cardabia Station, Carnarvon Basin, Western Australia.

Figs. 2, 4, 5, 7. *Giraliaster tertiarius* (Gregory). 2, 4, 5, lateral, adapical, and adoral view of SAM P18015. 7, adapical view of SAM P18014; both from Maslins Beach, Gulf St. Vincent, South Australia.


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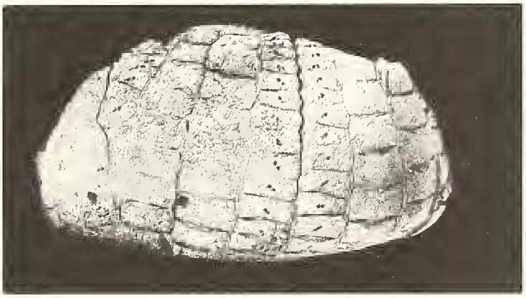
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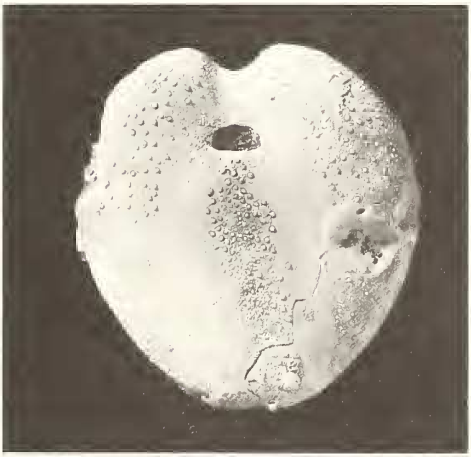
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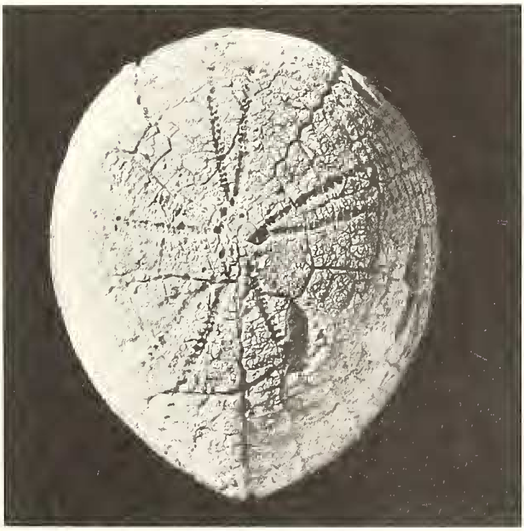
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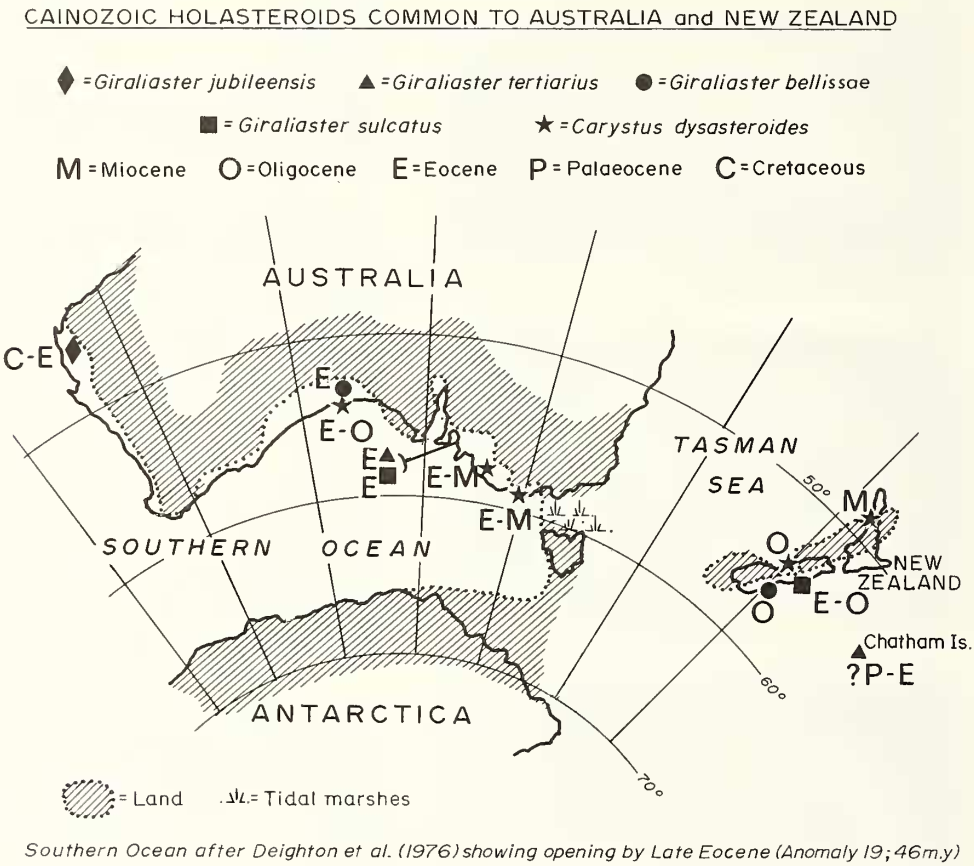
7

FOSTER and PHILIP, Tertiary holasteroid echinoids

the Southern Ocean. *Eupatagus laubei* Duncan from the late Miocene of western Victoria belongs to the living South African genus *Spatagobrissus*. This distinctive genus has previously been recognized only from the type species *S. mirabilis* H. L. Clark, a shallow-water spatangoid from the Cape Province.

The distribution of species of *Giraliaster* is more instructive. The genus appears first in the latest Cretaceous of the Carnarvon Basin, Western Australia. By the Eocene it was well established along the southern Australian coast and in New



TEXT-FIG. 6. Distribution of various Australian and New Zealand holasteroids superimposed on the reconstruction of Australia and Antarctica for the late Eocene as given by Deighton *et al.* (1976).

EXPLANATION OF PLATE 93

All figs. × 1.

Fig. 1. *Giraliaster tertiarius* (Gregory). Adapical view of holotype, BM E3382.

Figs. 2, 4. *Echinocorys australis* sp. nov. Adapical and adoral views of holotype, CPC F4818, Toothawarra Creek, Carnarvon Basin, Western Australia.

Figs. 3, 5. *G. sulcatus* (Hutton). 3, adapical surface of holotype, GSNZ EC690, Oamaru, New Zealand. 5, adapical surface of holotype of *Cardiaster latecordatus* Tate, SAM T286, Aldinga Cliffs, South Australia.

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Zealand (although *G. tertiarius* had reached the Chatham Islands apparently by the late Palaeocene or early Eocene). The other two species, *G. sulcatus* and *G. bellissae*, occur later in the New Zealand sequences than in southern Australia. The same pattern is seen in the more common species *Corystus dysasteroides* which was well established in southern Australia in the late Eocene, but does not appear in New Zealand until the late Oligocene.

Deighton *et al.* (1976, figs. 9–14) have reconstructed the development of the southern Australian continental margin from the time of the commencement of sea-floor spreading between Australia and Antarctica (53–54 my), and initiation of the deep-water circum-Antarctic current (30 my). They describe (p. 30) a complete land block between the expanding Southern Ocean and the Tasman Sea, formed by Tasmania and the South Tasman Rise. They suggest (p. 33) that shallow-water breaching of the South Tasman Rise took place in the Lower Oligocene (38 my in their fig. 13) allowing erosive, high velocity, but low-volume currents to cross the ridge from west to east. Text-fig. 6 summarizes their reconstruction for the late Eocene, prior to establishment of their marine connection between the Tasman Sea and the Indian Ocean.

The available evidence suggests that *Giraliaster* originated in the Indian Ocean area, and colonized New Zealand via southern Australia (text-fig. 6). The fact that New Zealand and Australian species of *Giraliaster* and *Corystus* may be conspecific strongly suggests colonization directly across the Tasman Sea rather than by a 12000 km journey around the north of the Australian continent. As the genus reached New Zealand in the late Palaeocene or early Eocene (about 50 my), it is therefore suggested that at least the first intermittent shallow-water connection between the Southern Ocean and Tasman Sea must have dated from prior to this time.

Trans-Tasman migration of echinoids from west to east is well established throughout the late Cainozoic, usually with the genera first appearing in the Australian sequences. *Evechinus chloroticus* is the commonest and most widespread littoral urchin inhabiting the present-day New Zealand coast and is recorded back into the Pliocene. However, the genus occurs in southern Australia only in the late Miocene where it is represented by *E. palatus*. *Fellaster zelandiae*, another New Zealand littoral species, is again recorded as fossil back to the Pliocene of New Zealand. *F. incisa* from the early Pliocene and Pleistocene of Victoria is the sole Australian representative of the genus.

Fell (1953) notes that with regard to living urchins the eastward migration has been from eastern Australia towards northern New Zealand, particularly to northern extensions of the North Island. Common Australian species, such as *Centrostephanus rodgersii*, *Holopneustes inflatus*, and *Heliocidaris tuberculata* occur in small colonies at various places north of Auckland. On the other hand, corresponding living New Zealand echinoids are unknown from Australia.

The available evidence indicates that trans-Tasman migrations of echinoids to New Zealand proceeded throughout the entire Cainozoic.

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